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ON THE ORIGIN OF THE GALAPAGOS ISLANDS.

BY G. BAUR.

(*Continued from page 229.*)

I STARTED with the sentence that continental islands must have a harmonic flora and fauna. In the Galapagos we found absolute harmony; my conclusion, therefore, is: *The Galapagos are continental islands, originated through subsidence;* they all formed at a past period one large island, and this island itself was at a still former period in connection with the American continent. This result is in direct opposition to the opinion of all authors who have worked on this group of islands, like Darwin, Hooker, Salvin, Grisebach, Engler, M. Wagner, Wallace, Peschel. All declare that these islands are of recent volcanic origin, that they have emerged out of the sea through volcanic activity, and that they have become peopled from the continent successively. Henri Milne-Edwards alone holds a different opinion; he believes that the Galapagos represent the remains of a former continent, and in this opinion I agree.

The principal reason of the believers of the elevation theory is the volcanic condition of the islands. But I do not see any difficulty in that. If mountain ranges like the Himalayas, the Alps, the Andes, the Rocky Mountains, could be elevated thousands and thousands of feet, why could not subsidence take place in other places? If Central America should disappear by-and-by through subsidence, the result would be that the tops of the highest mountains would form volcanic islands, some with still active volcanoes. This would be exactly the condition we see to-day in the Galapagos. I think, therefore, that the volcanic nature of a group of islands is no positive proof of its recent origin. Such groups of islands can be just as well considered as formed by the tops of the volcanic mountains of a sunken part of a continent.

But at first let us consider how the facts of the distribution of flora and fauna agree with the elevation theory. Islands which emerge from the sea can only be peopled accidentally, and must have a disharmonic flŏra and fauna. This is seen in all such islands, like the coral islands, which originated in this way. But in the Galapagos we found absolute harmony. Besides that we would have the greatest difficulty in explaining the presence of such peculiar forms as the gigantic land tortoises and the large lizards and the snakes, and so on; and again we would have the greatest difficulty to explain the peculiar distribution of the forms, and their peculiar differentiation on the more peripheral islands. To take only one example, how is it imaginable to explain the presence of these gigantic tortoises, some of which reach a weight of 700 pounds? They have not been introduced by man. When the islands were discovered by the Spaniards in the sixteenth century they were present in enormous numbers, like the other animals. According to the elevation theory we can only think of an accidental importation of these tortoises by some current, because they are quite unable to swim. After the islands had been elevated from the sea, and some vegetation had found its place there, it happened once, by a peculiar accident, that a land tortoise was carried over to the island. Alone it was helpless; it could not propagate. This was only possible after a similar accident imported another specimen *of the same species, of the other sex, to the same island.* Or we could imagine that at the same time animals of both sexes were thus accidentally introduced. By this we could at least explain the population of a single island. But how did all the other islands become populated? To explain this we would have to invoke a thousand accidents. But how can we explain that the members of one genus reached all the islands, and again those of another genus all the islands? *How can we explain that each island has a peculiar form of these genera? With one word, how can we explain the harmony of distribution by the theory of elevation?* All this is simply unexplainable by this theory.

The theory of subsidence, however, explains every point in an absolutely easy manner. All islands were connected together at a former period; at this time the number of species must have been small; through isolation the peculiar specialization of the species began; an originally single species was differentiated in many different forms; every island developed its peculiar races.

What seems to me to be a support of the subsidence theory is the fact mentioned by Wolf, that the flora of the Galapagos at elevations of about 900 feet is typically that of the Andes at an elevation of 9,000 feet. How could this alpine flora be explained by the theory of elevation; what is the reason that plants characteristic of an elevation of 9,000 feet are found at an elevation of 900 feet? This peculiar fact is also explicable by the theory of subsidence. I have shown above that an elevation of 300 fathoms, or 550 m., would bring together all the central islands. There are two lines of soundings made by the Fish Commission Steamer "Albatross," one between the Galapagos and Panama, and one to Acapulco. The deepest sounding of the first line is 1,927 fathoms (3,470 m.), at 6° 44′ N., 80° 27′ W.; that of the other is 2,256 fathoms, at 11° 45′ N., 97° 3′ W.

We need only an elevation of about 10,000 feet to connect the Galapagos with America. This would give the highest mountain on the Galapagos an elevation of 14,700 feet. This height is reached by many mountains and very often surpassed. The elevation of 900 feet on the Galapagos of to-day would correspond to an elevation of 10,900 feet. This is, of course, only an approximate value, which may be less or more. But there is no very great difficulty in adopting such an amount of subsidence.

The next question is, Is it not possible to determine during which geological period this subsidence of the Galapagos group, which we have to accept, has taken place? If any form becomes isolated for long a time it preserves the original general character that it possessed at the time of its isolation. This we see very well exemplified by the study of isolated dialects of a language. *I believe, therefore, that the peculiar genera we find to-day on the Galapagos have not originated there, but have been preserved in their old condition.* Let us again take the tortoises as an example. The tortoises found on these islands belong to the true land tortoises Testudinidæ; they represent, together with the forms from the islands round Madagascar and the peculiar Manouria from India and the Sunda Islands, the oldest living representatives of the family. The paleontological history of the Testudinidæ reaches back to the Bridger Eocene. From this formation the oldest land tortoise, Hadrianus, has been recorded, which is nearly related to Manouria, characterized by the double caudal-shield, as in the Emydidæ. Forms very much like those from the Galapagos we find in the Miocene. *We do not go too far to say that it is probable that during the Eocene period, and possibly a little later, the Galapagos were still in connection with the continent.*

The important question is, Where was this connection? In their general characters the fauna and flora of the Galapagos show resemblances to the great Mexican and Sonoran province, and also to the West Indies. And it may be that the connection was with these regions (and it seems more probable than any other), but of course it is quite impossible to bring to-day any positive proof for this idea. It would appear that the whole west coast of America has undergone subsidence. We find there a great number of islands: Prince Wales, Queen Charlotte, Vancouver, Santa Barbara, Guadaloupe, and so on. That all these islands have been in connection with the continent at a former period seems to be certain. They appear as the result of subsidence. The Revilla Gigedo Islands are in the line of this sunken district. Farther south we find the small island Clipperton, and in a southeastern direction the Galapagos. Between Clipperton and the Galapagos two islands, Duncan and Galego, have been recorded; but they are of a doubtful nature,—at least they have not been seen again in latter times. But could we not imagine that they have disappeared in the course of this and the last century by subsidence?

Near the Mexican coast we have the Tres Marias Islands. These are considered as continental even by Wallace; but the more distant Socorro of the Revilla Gigedos are considered by Wallace as oceanic. Wallace believes, therefore, in subsidence in regard to the Tres Marias, in elevation in regard to the Revilla Gigedos, simply because there are no mammals on the barren Revilla Gigedos, and because they are placed within the thousand-fathom line. The fauna of the Revilla Gigedos is typical of that of lower California and the Sonoran province, and I believe also that the

Revilla Gigedos are nothing but a part of the American continent; they are also, like the Galapagos, within the 4000 m. line.

South of the Galapagos we have the islands Felice and Juan Fernandez, with their peculiar flora and fauna. It is not possible to determine whether there has been any connection between these islands and the Galapagos, but the fact that we find on the Galapagos three forms of Antarctic animals, which reach the most northern limit in this group, is to be mentioned. These animals are the *Otaria jubata*, *Arctocephalus australis*, and the peculiar penguin, *Spheniscus mendiculus* Sundev., only found on the Galapagos. Another interesting point is that the albatross, which so far as I know has only been described as breeding from the southern islands, especially Tristan daCunha, breeds on Hood's Island, as observed by Delano and Wolf.

Much work remains to be done. A great number of systematic deep-sea soundings have to be made between these different groups of islands and the continent. And the islands themselves have to be examined very carefully. We know nothing at all about the fauna and flora of the isolated Clipperton Island and Malpelo; we hardly know anything about Cocos Island, which seems to be in many respects quite different from the others, having a more tropical appearance. An enormous and highly interesting field of research is here open. After all this has been done, we may be able to discuss fully the question of the connection of the different islands. One thing, however, we assume to-day: *the probability of the origin of the Galapagos through subsidence.* But if this be probable for the Galapagos, how is it with the Sandwich Islands, for instance; so far as they are known they seem to be of the same harmonic nature in flora and fauna. Have they not originated in the same way? How about the other islands in the Pacific, and how about the theory of the consistency of the Pacific Ocean? Is this theory really established on a sound basis?

We now come to another very important question, What is the reason of the variation of the forms on the different islands? In other words, What is the origin of the different species of the different islands?

Of all the forms from the islands, the genus Tropidurus is best known. The most divergent species of this genus we find on Abingdon on one side, and on Hood on the other. On Abingdon we also find a peculiar species of Nesomimus, of Certhidea, of Cactornis, of Testudo, and probably of Geospiza. On Hood Island we also find a peculiar species of Nesomimus, of Certhidea, of Geospiza (Cactornis has not yet been discovered), and of Testudo. These forms are entirely different from each other, and different from the forms of the central islands. What is the reason of this difference? The fact is that *all* forms of an island become modified, and not alone a single species; the plants and the different groups of animals all at the same time. *There must be a common cause which produces this effect. And this cause can only be looked for in the surroundings, in the physical conditions of each island.* That there is a difference among these islands is evident. All the lower islands do not reach the damp region; they must be therefore in quite a different physical state. Some of these islands are without a drop of fresh water; others are furnished with this element. This difference must have a different effect on the same forms of animal and vegetable life.

I have expressed the opinion that when these islands were still in connection, forming one large island, there was probably only a single species of Tropidurus, Testudo, Nesomimus, and so on. There were probably certain small local variations, but they were not so expressed, being not separated; and besides that any new characters appearing were checked by intercrossing. We could imagine, for instance, that the large island had the higher moist region over its whole extent; the effect would have been that humidity was spread more equally over the whole island. If a certain portion became separated, and lost that upper horizon, it was at once in a fundamentally different condition. This affected the flora and fauna; and the flora again the fauna. All these changes, of course, must have gone on *very gradually*.

From these considerations we may proceed to get an explanation of the variation. Hoffmann and others have succeeded, in the course of several years, in changing wild plants by cultivation in gardens. Thus Hoffman could change the wild carrot considerably, and this change became inherited. Let us consider what was done in this case. The wild carrot was isolated from the others, and brought under different conditions; it received, for instance, more food, and the effect was the change. It is exactly in the same way that we have to explain the change of forms on the different islands; an arid, dry island must have a different effect on an organism than a fertile and moist island. The different condition produces a different effect, and thus a different form. If the conditions were absolutely the same, the effect would be the same. Let us imagine that we have a form A, which has, and so have its ancestors, been for a long time in the same conditions. This form A will be represented at a certain moment by very numerous individuals of different age, between the egg and the senile stage. Now let us change the conditions; the change will affect this long series of individuals of the same species in a very different way. The new-born will react differently from the senile form. But among this long series of individuals there will be a certain number of organisms which will be *most plastic*, as I may express it, *to the stimulus of the new conditions*. The senile forms, for instance, probably are not affected at all; they die out through senility. Between these and the egg-stage, however, certain members must be in the condition which I call most plastic. The different individuals may be expressed according to their age, A^1, A^2, A^3, A^4, A^5, . . A^n.

A^n, the oldest individual, disappears by senility and A^{n-1} takes its place; the whole series is moved one line; the individuals of the greatest plasticity, for instance, do not remain the same, but are replaced by the next younger group. In this way a constant flow takes place, which continues until harmony is reached again between the individuals and the conditions.

I may explain this a little better by an example. The different stages of a plant, from the youngest to the oldest, may be expressed in a certain moment by A^1, A^2, A^3, A^4, A^5, . . A^n.

Now new conditions begin to appear, for instance, by the gradual disappearance of water. The result will be that the plant has to depend on less food than before; the large forms which have become so large through ample food will die out through senility;

others come in their place, but these will not develop so highly, because the necessary food is not given. The younger forms have to depend from the beginning on less food, and cannot grow to such extent as their ancestors ; the result probably would be the evolution of a smaller race. This will become constant as soon as it is in harmony with the surroundings. We can easily imagine a differentiation on the same spot, through the change of conditions ; but great effects are produced by isolation. If a part of the individuals of a certain form become separated, the slightest difference in the conditions of the new locality must work on the individuals, until harmony is produced. The absence of intercrossing of the separated forms will preserve the characters of each. I shall give an example for both cases, taken from the well-known communications of Vladimir Schmankewitsch.

Let us imagine that the brine shrimp (*Artemia salina*) is living in a salt-water lake which is supplied with fresh water by a river. Through some cause this river may be prevented from emptying its waters in the lake, being forced to take another course. The result will be that the water will increase gradually in density. By this gradual change *Artemia salina* will be transformed into *A. muhlhausenii.* Of course it is impossible that any adult Artemia is changeable ; but the changed conditions will have an effect on the egg and the younger plastic stages ; the old forms will disappear. The young ones will change until harmony with the surroundings is restored. Exactly the same will take place if *A. salina* is brought from its original locality to another place, in which the density of the water is greater than on the original locality. In the first instance a new species originates on the same spot, through the change of conditions ; in the second a portion of the individuals becoming isolated from the original stock develop into a new form.

This whole consideration is based on continuous growth, and on the fact that members of the same form are in a different stage of plasticity at a different age. If the harmony of a certain group is affected by the intercourse of any disturbing factor,—in other words, if the conditions are changed,—a general alarm is raised in the group until harmony is reëstablished. I may call this process the process of harmonic growth, founded on the plasticity of the younger individuals. I believe that most of the variation goes on in certain definite directions produced by the conditions, this word taken in the widest sense. I do not believe that species originate through indefinite variation, produced by the mingling of different germ-plasmas on which natural selection works. I am inclined to believe that any change must stimulate the organism, and I think it is this stimulus which affects the germ-plasma just as well as the somatic plasma, if we want to make any such artificial distinction.

Perhaps we may be allowed to make some remarks in this connection about the inheritance of acquired characters. If any form shows a new character produced during the lifetime of the form, and not dependent upon any portion of the germ-plasma, we speak, in Weismann's meaning, of an acquired character of this form. I may use a very clear example, taken from Darwin: "The natives of the Amazonian region feed the common green parrot (*Chrysotis festiva* L.) with the fat of large Siluroid fishes, and the birds thus treated become beautifully variegated with red and yellow feathers. In the Malayan Archipelago the natives of Gilolo alter, in an analogous manner, the colors of another parrot, namely the *Lorius garrulus* L., and thus produce the Lori rajah or King Lory. These parrots in the Malay Islands and South America, when fed by the natives on natural vegetable food, such as rice and plantains, retain their proper colors."

Now here we have an acquired character. Will it be inherited? Certainly not, if the animal is fed with its natural food; but it will *appear again* when the animal receives the food producing the peculiar color. Another example: If an alpine plant is transported to a botanical garden, and has become different from the alpine form, it has acquired a new character. The question is, Is this character "inherited" by the next generation? The answer will be *yes*, if the conditions that produced this new character remain; for instance, if we leave the plant in the botanical garden. The answer will be *no*, if we change the conditions that produced that new character; for instance, if we bring the plant back to its original locality.

Hoffmann has given to the wild carrot a new character through long cultivation; this character has become inherited,—that is to say, seeds of the plants showing this acquired character show it again if placed in the same conditions. But let us plant the seeds in the original place; they do not receive the food they had in the cultivated ground, and will in a very short time fall back to the original wild state, simply, as it seems, because the conditions under which the character appeared are not given any more. The word inheritance is very often used in an absolutely wrong and misleading way. We cannot speak of direct inheritance of an acquired character; what is called here inheritance is simply the reappearance of the acquired character under the same stimulus; it is not, strictly speaking, inherited. For instance, we cannot say that the reduction of the biting muscles of lap-dogs is directly inherited. The biting muscles are simply kept low by the effect of the peculiar soft food that these animals receive, and by their peculiar mode of living; but if we change the food and bring the animal into different conditions, these muscles will increase again.

Inheritance is somewhat comparable to reflex motion and automatic motion. Inheritance in its beginning is comparable to reflex motion,—that is to say, a certain character appears under a certain stimulus. Inheritance is comparable to automatic motion when a certain character appears without that stimulus. In other words, the germ is first reflective, then automatic.

The difference between my opinion and that of Weismann is this: According to Weismann, the mingling of germ-plasma of different individuals produces variation, on which natural selection acts. According to my opinion, variation is the product of the stimulus of the conditions on the germ and somatic plasm; it is therefore definite. Variation goes on in certain definite lines. It is the surroundings which change the germ and somatic plasm, which determine variation.

That variation goes in definite lines, determined by the conditions in which the organism lives, is admitted by all those who ever studied species; I mean by all those who studied, for instance, all the representatives of a single genus and its geographical distribution; the researches of Joel A. Allen and Dr. Merriam are highly instructive in this line. It is also admitted by nearly all paleontologists. I have expressed the opinion that "inheritance" takes place only after a very long repetition of the same stimulus on an organism. Why is it not imaginable that under *certain* conditions, when the organization, instead of receiving an endless repetition of a stimulus, suddenly receives a single most effective stimulus, that the effects are inherited, and appear for some generations? I do not want to be misunderstood; I do not believe in the general inheritance of mutilations; nobody can believe in such a theory. But that certain mutilations, under certain conditions, *may be inherited*, this I think is a possibility which cannot be entirely neglected. And we have to consider such cases, dark and unexplainable as they appear. Of course, in the origin of species, I do not think that this question is of any importance, If even certain mutilations in nature would become inherited, they could not have any influence whatever on the great harmonic number of the same species. I do not think that a species has ever been developed through inheritance of a mutilation. I think we are yet far from understanding the true nature of inheritance.

The objection will be made to me that I do not consider the sexes at all. To this I may reply that I am not inclined at present to lay so much stress on the effects of the mingling of different germ-plasmas. This mingling doubtless produces slighter or greater individual variation, and is certainly one factor of variation. But we have to consider that nearly all our researches on variation in this respect are based on domesticated organisms, which are, of course, under entirely different conditions from those in free nature. I can only think that certain even apparently most useful variations, created by the mingling of the germ-plasmas, must soon be swallowed up by the governing mass of harmonic forms, and are thus generally unable to develop a new branch. I consider sexual union more as a *stimulative* than a *formative* factor. *The same causes that produce variation in asexual animals must produce variation in sexual animals.* What we have to do is to study species and variation in nature; to study their conditions of life, their surroundings; to find out how these are in relation to each other. Such a work, in fact, has never been done. Dr. Merriam has undertaken such a task, however, for some of the American mammals.

There is no other place on the whole earth which affords better opportunities for such a work than the Galapagos. Here we have the original natural conditions, hardly influenced by man. If all the variations of the forms on this group of islands, or even only the variations of a few genera, are studied, and the conditions of each variation are examined, then we may perhaps be able to express a more definite opinion on the causes of variation itself. Such work ought to be done *before it is too late.* I repeat, before it is too late! Or it may happen that the natural history of the Galapagos will be lost, as it has unfortunately been lost in so many islands; for instance, of St. Helena and the Mascarenes, lost forever, irreparably!

If I can succeed in raising the necessary funds, I shall try to do something for the solution of this important question. A visit of several months would bring out a good deal of light. The question of the origin of the islands themselves could be solved by the most careful collections of the flora and fauna of each, even the smallest island. The conditions of the flora and fauna as well as the domesticated animals which have become wild, could be studied on the spot. I may make some remarks upon this point. The following animals have become wild on the Galapagos, according to Wolf: Cattle, goats, horses, asses, hogs, dogs, cats, chickens. Cattle are found wild on Charles (8–900); Chatham (2–3000); South Albemarle some; horses only on Charles Island; and asses are very numerous on Charles, Chatham, Indefatigable, and Albemarle. They live together in troops of ten to fifteen. Why, Dr. Wolf asks, have these animals adopted the peculiar habit of sitting on the hind legs like a dog or a cat? And he adds that the most learned man could not help laughing at seeing these animals in this peculiar position. Goats are said to have diminished on account of the dogs. They are found on the arid mountains of Charles, Chatham, and Barrington. Hogs occur on all larger islands. Dogs live in droves in the upper and lower regions. The wild-cats on Charles and Chatham are all black,—a peculiar fact, since this color is hardly ever seen in Ecuador. They live in the roughest fissures of the lava near the coast, hunting for crabs and fishes. Chickens are found on the highest most inaccessible regions of Charles. Also here a great field of research is open.

But besides these questions of general interest, some special points could be studied. For instance, material could be collected for the embryology of the penguin, the frigate-bird, the albatross, the seals, the Iguanidæ, and the large myriapod Scolopendra.

"The ground is classic ground," says Mr. Salvin, "and the natural products of the Galapagos Islands will ever be appealed to by those occupied in investigating the complicated problems involved in the doctrine of the derivative origin of species."

But beside studies in nature, we need experiments; biological experimental stations would be of an enormous help in the question of variation. Our means of communication and transportation are so highly developed to-day that it is easy to get animals and plants from very remote places in short time; by bringing these organisms in different conditions a great number of very valuable experiments at least could be made.

I will finish these considerations, which I hope will be taken for what they are,—*ideas—not definite opinions*,—with a word from Darwin, in a letter to M. Wagner:

"In my opinion, the greatest error which I have committed has been not allowing sufficient weight to the direct action of the environment,—*i. e.*, food, climate, etc.,—independently of natural selection."

Clark University, Worcester, Mass., December 6th, 1890.

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